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The Crescent of Foramina in *Australopithecus afarensis* and Other Early Hominids

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ABSTRACT The crescent of foramina of the cerebral surface of the sphenoid bone (superior orbital fissure, foramen rotundum, foramen ovale, foramen spinosum) differs morphologically in the African great apes and modern humans. New discoveries of *Australopithecus afarensis* at Hadar, Ethiopia, draw attention to the similarity of the crescent, particularly the "foramen" shape of the superior orbital fissure and its close proximity to the foramen rotundum, in this species, the African apes, and many other primates. *Australopithecus africanus* also shows this primitive pattern, whereas "robust" australopiths and humans share a configuration in which a true, laterally extended superior orbital fissure intervenes between the greater and lesser wings of the sphenoid and a broad bridge of bone separates the fissure from the foramen rotundum. This shared morphology may be added to the list of putative "robust" australopith–*Homo* synapomorphies.

The so-called "crescent of foramina" (Grant and Basmajian, 1965) consists of foramina that are situated within the sphenoid bone and follow a curved, crescent-shaped path on both sides of the sella turcica. The arched sequence of apertures (whose crescent shape can be seen only in a cerebral view) includes the superior orbital fissure (the crescent's superolateral end), the foramen rotundum, the foramen ovale, and the foramen spinosum (the crescent's inferolateral end). The African great apes differ from modern *Homo sapiens* in several aspects of the crescent and the adjacent area, as recognized nearly 150 years ago by Richard Owen in his classic descriptions of chimpanzee and gorilla skulls (Owen, 1849).

The recently augmented sample of *Australopithecus afarensis* from Hadar indicates that this early hominid shares much of the morphology of this region with the African great apes. This finding led us to examine other early hominid crania for the status of this feature. We found that whereas *A. afarensis* and *A. africanus* share an apparently primitive morphology with the African great apes, "robust" australopith species and *H. sapiens* share a derived state.

The superior orbital fissure faces anteriorly, permitting the passage of nerves between the middle cranial fossa and the orbital cavity. In humans this elongated, comma-shaped fissure forms a gap between the greater and lesser wings of the sphenoid bone. The medial, and widest, part of the fissure is on the same sagittal plane as the foramen rotundum; from there the fissure extends superolaterally about 1.5–2 cm and gradually narrows. Often, however, the fissure has a blunt, club-shape termination (Figs. 1,2). Lateral to the fissure's apex, a

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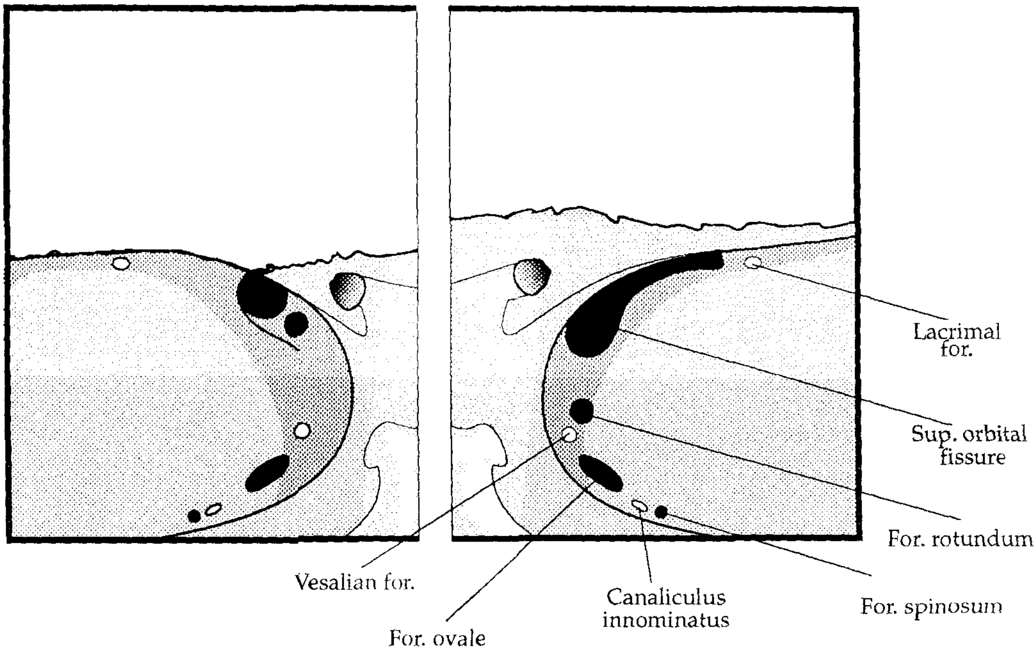

Fig. 1. A cerebral view of the crescent of foramina in a gorilla (left) and a modern human (right). Note the difference in the morphology of the superior orbital fissure, in the relative position of foramen rotundum and in the lateral extension of the lesser wing of the sphenoid. In addition to the fissure, foramen rotundum, foramen ovale, and foramen spinosum, three other foramina occasionally appear, independent of each other, as part of the crescent. These apertures are the lacrimal foramen, which, when present, is the first in the crescent's chain and is lateral to the apex of the superior orbital fissure; the vesalian foramen, which lies between the foramen rotundum and the foramen ovale; and the canaliculus innominatus, found between the foramen ovale and the foramen spinosum. The lacrimal foramen permits an anastomosis between the lacrimal artery and the anterior branch of the middle meningeal artery; the Vesalian foramen carries an emissary vein; and the canaliculus serves as an outlet for the lesser (superficial) petrosal nerve. The optic foramen, which also lies within the sphenoid bone, is medial to the superior orbital fissure and is not considered part of the crescent of foramina.

suture "welds" the gap between the greater wing and the lesser wing. It is the medial part of the superior orbital fissure that serves as the outlet for cranial nerves (CN) 3, 4, and 6, and for the ophthalmic branch of CN 5. The foramen rotundum faces anteriorly, permitting the passage of the maxillary branch of CN 5 to the roof of the pterygopalatine fossa and to the inferior orbital fissure. The foramen ovale and foramen spinosum face inferiorly. The former carries the mandibular branch of CN 5 to the infratemporal fossa, and the latter allows the passage of the middle meningeal artery into the cranial cavity.

The African apes do not exhibit the long, narrow superior orbital fissure. Instead, there is a round foramen, whose lateral margins fall on the same sagittal plane as the foramen rotundum or even medial to it. We confirmed this configuration on a sample of 30 chimpanzee and 30 gorilla skulls of both sexes in the Adolph Schultz collection at the University of Zurich. A close examination of the region reveals that, compared to modern humans, the great apes have a tendency toward short lesser wings of the sphenoid bone. This is especially true in the gorilla, where the short process that is homologous to the lesser wing extends laterally no farther than the superior orbital foramen. (Nearly the entire length of the greater wing is thus in direct contact with the frontal bone; see Fig. 3, upper.) The lateral margins

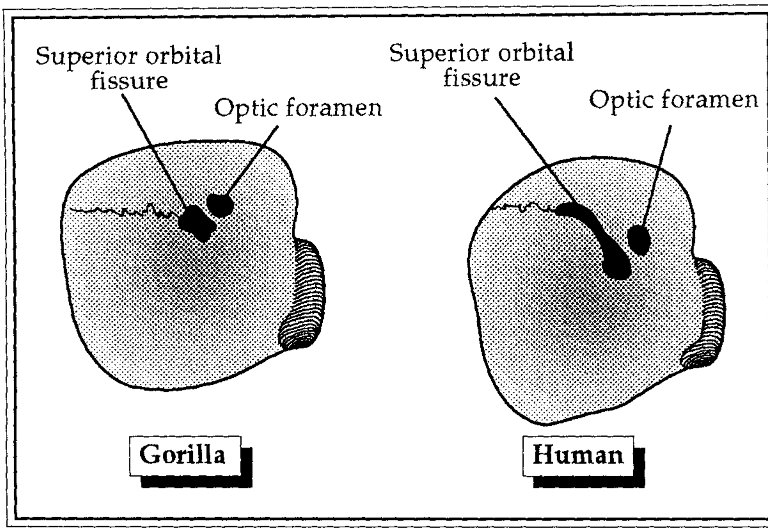

Fig. 2. An orbital view of the superior orbital fissure and the optic foramen in a gorilla and a modern human, right side. Adapted from Grant and Basmajian (1965: Fig. 69).

of the foramen were seen to be pinched in some of the skulls (more so in the chimpanzees than in the gorillas), resulting in a teardrop shape of the foramen. However, none of these foramina come close in shape to the elongated, comma-like appearance of the superior orbital fissure in humans. The absence of a fissure-like foramen in the African apes and in many other primates suggests that the round foramen is the primitive character state. This condition is apparently what leads Grant and Basmajian to state that "in man it is the *medial or primitive* part of the fissure that the nerves crowd through" (1965: 529, emphasis added).

The different configurations seen in the African apes and in modern humans make the anatomy of this region interesting in early hominids. However, this region is rarely available for observation in fossil specimens because, on the one hand, the fragile nature of the bony plates deep in the orbits and of the sphenoid sinus walls (especially in adults, where pneumatization is extensive) hinders preservation, and, on the other, paleontologists tend to be reluctant to remove the matrix from these delicate, convoluted anatomical structures.

Enough of the area has been preserved in three *A. afarensis* specimens to shed light on the crescent of foramina in this species. However, it was only the recent discovery of the third specimen—A.L. 417-1 (Kimbel et al., 1994)—that drew our attention to the phenomenon and to the fact that the configuration strongly resembles that found in the African apes, especially the chimpanzee (see below). The three *A. afarensis* specimens, A.L. 58-22, A.L. 333-105 (the infant specimen), and the newly discovered A.L. 417-1, are quite fragmentary, yet they clearly exhibit all the components of the crescent. One immediately notices that the superior orbital "fissure" is a vertical, oval foramen rather than a laterally elongate, comma-shaped fissure. In specimen A.L. 58-22 (Fig. 3, lower), a cerebral view exposes the entire circumference of the superior orbital foramen, whose lateral margins are at approximately the same sagittal plane as that of the foramen rotundum. The vertical oval shape of the superior orbital foramen brings its inferior margin so close to the foramen rotundum that only an exceedingly thin bridge is left between them—just as in the African apes (Fig. 3) and quite unlike the wide strip of bone that separates these two structures in modern humans. The superior orbital foramen in A.L. 58-22 narrows to a laterally extended, suture-like connection between the lesser and greater wings of the sphenoid. In this specimen the lesser wing (indicated

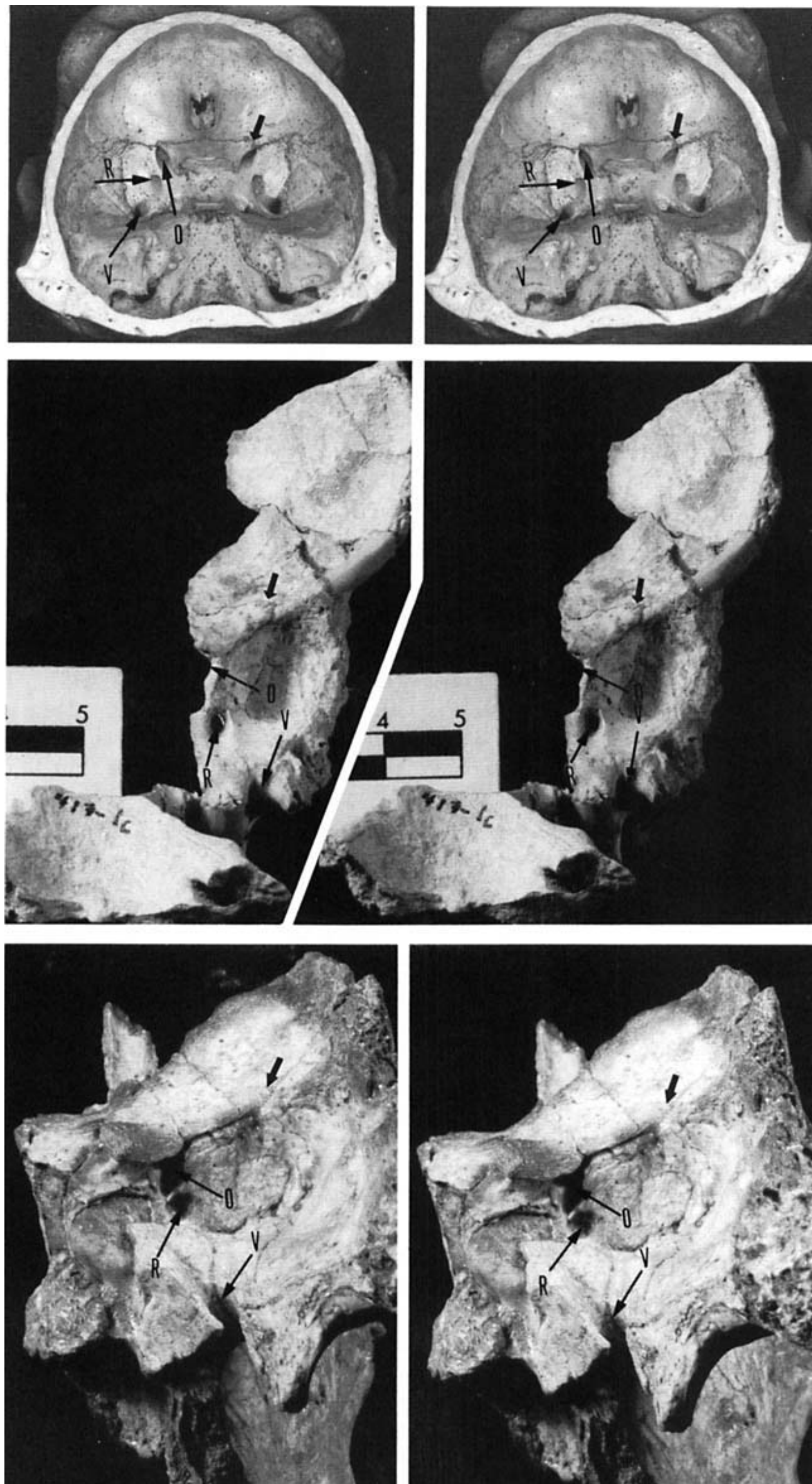

Fig. 3.

by the arrowhead in Fig. 3, lower) extends laterally as far as the midpoint between the foramen and the inner calvarial wall. In this respect, *A. afarensis* seems to resemble the chimpanzee more than the gorilla, as in the chimpanzee the lesser wing usually extends laterally much farther than in the gorilla, approaching the relative length of the human lesser wings.

In A.L. 417-1d the vertical lateral margin of the superior orbital foramen, its narrow, suture-like lateral extension, the very thin bridge between the superior orbital foramen and the foramen rotundum, as well as the abbreviated lesser wing, are all clearly seen (Fig. 3, middle). The infant specimen A.L. 333-105, although imperfectly preserved in this region, also exhibits this suite of features. The immaturity of this specimen is of interest because in early ontogenetic stages modern humans exhibit an even larger and more extensive superior orbital fissure than do adults (see, e.g., Warwick and Williams, 1973).

Broom (1947) drew attention to the morphology of the anterior cranial fossa of *A. africanus* specimen Sts. 5, but he made no reference to the state of the crescent of foramina. In the late 1970s, two of us (Y.R., W.H.K.) independently were able to examine Sts. 5 while the calotte was briefly separated from the base. We are able to confirm Broom's (1947) Figure 1, which depicts the chimpanzee-like (as compared to the gorilla) extended lesser wings of the sphenoid, and can record that the distance of the foramen rotundum from the superior orbital fissure is very small. [Unfortunately, our notes do not record the state of the superior orbital fissure itself, although we predict that it will be in the form of a foramen. R.J. Clarke (personal communication) and C.A. Lockwood (personal communication) inform us that although the superomedial part of the crescent is not well preserved in Sts. 5, there is no evidence of a laterally extended fissure as in humans.) Two other *A. africanus* specimens clearly reveal the primitive pattern documented in *A. afarensis* and the chimpanzee. Craniofacial fragment MLD 6 presents a superb view of the region under discussion, and most of the elements of the primitive configuration are also preserved on the recently discovered *A. africanus* cranium Stw. 505 (cast observation).

In specimen Sts. 19, which we have elsewhere attributed to *Homo* sp. based on temporal bone morphology (Kimbel and Rak, 1993), the foramen rotundum is present immediately inferior to the sharp crest on the sphenoid that divides the middle from the anterior cranial fossa; the foramen cannot have been separated from the missing superior orbital foramen/fissure by more than the thinnest bridge of bone. In this early *Homo* specimen, at least, it seems that the primitive pattern is retained. Tobias (1991:138) describes *H. habilis* cranium OH 24 as having a doubled foramen rotundum: "(the two openings) lie close together, one above the other, the upper being the smaller of the two. Between them the bone crowds in from medial to lateral to form a bony partition completely separating the two moieties from each other." No mention is made of the state of the superior orbital fissure, but we wonder whether what is described in OH 24 as a doubled foramen rotundum is actually a single foramen rotundum intimately associated with a superior orbital *foramen*. The skull cap of this specimen was glued back after restoration, thus blocking access to the relevant region for a new inspection (R.J. Clarke, personal communication). To our knowledge, no other specimen of *H. habilis* or *H. rudolfensis* either preserves or permits access to this region of the endocranium.

The morphology of the crescent of foramina in *A. afarensis* and *A. africanus* is of interest not only because of its primitive pattern, but because, surprisingly, the available "robust" australopith specimens show most of the elements associated with the modern

Fig. 3. Stereoscopic photographs of a cerebral view of a female gorilla (upper, ca. 1/3 natural size), the *A. afarensis* specimens A.L. 417-1 (middle, natural size) and A.L. 58-22 (lower, natural size). Note the superior orbital fissure (O), the foramen rotundum (R), the foramen ovale (V), and the sphenofrontal suture (indicated by an unlabeled arrow). Note that, whereas in the gorilla there is no lesser wing, in the *A. afarensis* specimens the lesser wing extends laterally about halfway to the calvarial wall, as in the chimpanzee. Also note the close proximity of foramen rotundum to the superior orbital foramen in all three specimens.

TABLE 1. List of the fossil hominid and modern African ape specimens that provided the anatomic information discussed in the text

Specimen	Provenance	Taxonomic affiliation	Character state
A.L. 417-1d	Hadar, Ethiopia	*A. afarensis*	Foramen
A.L. 58-22	Hadar, Ethiopia	*A. afarensis*	Foramen
A.L. 333-105	Hadar, Ethiopia	*A. afarensis*	Foramen
Sts. 5	Sterkfontein, South Africa	*A. africanus*	Foramen (?)
MLD 6	Makapansgat, South Africa	*A. africanus*	Foramen
Stw. 505	Sterkfontein, South Africa	*A. africanus*	Foramen
Sts. 19	Sterkfontein, South Africa	*Homo* sp.	Foramen (?)
OH 24	Olduvai, Tanzania	*Homo habilis*	Foramen (?)
KNM-WT 17400	West Turkana, Kenya	*A. boisei*	Fissure
KNM-ER 407	East Turkana, Kenya	*A. boisei*	Fissure
KNM-WT 17000	West Turkana, Kenya	*A. aethiopicus*	Fissure
Common chimpanzee (n = 30)	The Adolph Schultz collection at the University of Zurich, Switzerland	*Pan troglodytes*	Foramen
Lowland gorilla (n = 30)	The Adolph Schultz collection at the University of Zurich, Switzerland	*Gorilla gorilla*	Foramen

human pattern. In only two specimens of *A. boisei* (KNM-WT 17400 and KNM-ER 407), plus the single cranium of *A. aethiopicus* (KNM-WT 17000), is the crescent accessible. It is best preserved in KNM-WT 17400, where the comma-shaped superior orbital fissure extends laterally beneath the lesser wing of the sphenoid and a considerable distance separates the fissure from the foramen rotundum. In KNM-ER 407 the crescent is not well represented (all the margins of the superior orbital fissure are broken), but the human configuration is expressed on the floor of the middle cranial fossa through the large distance to the foramen rotundum. A positive cast made from the endocast of KNM-WT 17000 (kindly supplied by Dr. Alan Walker) indicates the same pattern: the medial end of the fissure is partly obscured by matrix, but there is no doubt that a vertically oriented foramen (as described in *A. afarensis*) is absent here, and, moreover, there is a large distance to the foramen rotundum.

In most of the anatomical structures of the crescent of foramina, *A. afarensis* and *A. africanus* emerge as almost indistinguishable from the chimpanzee. The apparent human morphology of the "robust" australopith crescent adds yet another character to the list of putative craniodental synapomorphies uniting the "robust" australopiths and *Homo* in an exclusive sister group relationship (e.g., Dean, 1986; Walker and Leakey, 1988). Whether these similarities genuinely signal regency of phylogenetic descent or are the product of homoplasy is a question still open to debate, as several recent analyses (e.g., Skelton and McHenry, 1992; Wood, 1991) found it to be. The paucity of informative crania makes it impossible to specify the character state(s) in the crescent of foramina for the early species of the *Homo* clade. Such information obviously is critical to determining the likelihood that the apomorphic "human" pattern arose more than once in hominid evolution.

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mens for us, although their interpretations may differ from our own. We thank Dr. Alan Walker for providing us with a positive cast of the sphenoid bone prepared from the endocast of KNM-WT 17000 and Professor Tobias for providing us with a cast of Stw. 505. Observations on the African ape specimens were carried out at the Department of Anthropology of Zurich University, in Zurich, Switzerland.

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